Running head: Temporal tuning of balance retention and tactile processing

Visual perturbations temporally tune balance retention and associated tactile processing

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Abstract

Predictive processes are key components for the sensorimotor control of human movement. One characteristic phenomenon that arises around human movement is that somatosensory processing on moving limbs is modulated by being either enhanced or suppressed. This modulation is thought to arise from an interplay in the reliance between predictive and feedback signals that are relevant for the action. While this interplay can characterize tactile modulation during upper-limb goal-directed movements, less is known about how it functions during complex whole-body movements in dynamic environments. We here examine tactile modulation during upright stance that can be visually perturbed in a predictable or unpredictable manner. Participants were immersed in a virtual room, which could move in a predictable or unpredictable manner. We probed tactile processing via a vibrotactile stimulus delivered to the participants' calf muscle, through which we assessed detection thresholds shortly before and after the perturbation. Meanwhile, human movement was assessed by measuring the center of pressure and head kinematics. As expected, anticipatory postural behavior preceded the predictable perturbations, whereas postural reactions were evident after both perturbation types. Tactile processing was hampered whenever participants were standing quietly relative to a sitting baseline. Tactile processing was not modulated by the predictability of the perturbation, but it was temporally tuned throughout the task, being enhanced after the onset of the perturbation. These results demonstrate that tactile signals can be dynamically modulated during complex whole-body movements, supporting the notion that tactile processing reflects an interplay between predictive and feedback signals.

Keywords: Perception & action; Postural adjustments; Tactile modulation; Virtual reality

New and noteworthy

We demonstrate temporal modulation of tactile processing at lower limbs during postural responses to visual perturbations. Tactile signals are generally suppressed during standing than sitting, but this suppression recovers shortly before the body is about to respond to a visual perturbation that challenges upright stance. Our results suggest that tactile processing during balance retention within complex environments is modulated by an interplay between feedforward and feedback signals.

Introduction

Tactile sensitivity is reduced on a moving limb compared to the same but static limb. This tactile suppression is built on the idea that motor commands are used to predict future sensory states of the body, and then the sensory feedback that matches the prediction is eventually suppressed (Blakemore et al., 2000). This has been demonstrated not only for self-caused sensations, such as self-tickling (Blakemore et al., 2000) or force-production (Shergill et al., 2003), but also for external sensations that arise on one's own moving limb (Fuehrer et al., 2022). In other words, externally-generated tactile stimuli that are presented on one's own moving body are perceived as weaker compared to the same stimuli presented on the same but static body (Voss et al., 2008; Buckingham et al., 2010; Voudouris & Fiehler, 2017). Although tactile suppression may be partially explained by peripheral mechanisms (Williams & Chapman, 2002; Seki & Fetz, 2012; but see Broda et al., 2020), central predictive processes contribute to this phenomenon (Haggard & Whitford, 2004; Voss et al., 2008; Arikan et al., 2021; Fuehrer et al., 2022; but also Press et al., 2023).

Human movement planning and control primarily depends on the integration of feedback signals with feedforward predictions (Desmurget & Grafton, 2000). In this sense, humans establish predictions about the underlying dynamics based on the current sensory feedback and prior information about the state of their own body and the environment. Thus, the level of tactile suppression should be proportional to the quality of the prediction or the certainty of the environment. Indeed, tactile suppression recovers when sensory guidance of the reaching hand becomes important (Voudouris & Fiehler, 2021). Likewise, it is substantially reduced when grasping objects of unknown dynamics, which requires increased tactile feedback processing to successfully interact with the object (Voudouris et al., 2019). These suggest that tactile suppression is not an all-or-nothing mechanism, but rather a dynamic process that depends on the interplay between predictive and feedback signals.

Most of the work on tactile suppression has been conducted in rather simple finger (Williams & Chapman, 2002), or more complex upper-limb reaching (Buckingham et al., 2010; Voudouris & Fiehler, 2017), grasping (Manzone et al., 2018; Voudouris & Fiehler, 2022), and lower-limb (Morita et al., 1998) movements. We are here interested in examining whether this interplay of predictive and feedback mechanisms generalizes to more complex whole-body movements in dynamic environments. While continuous sensory integration is crucial for postural control (Peterka, 2002; Chiba et al., 2016), less is known about how sensory signals from the standing body are modulated when the sensorimotor system is confronted with misleading sensory information. When standing, cutaneous signals from the foot are integrated in the motor plan for the upcoming initation of a step (Mouchnino & Blouin, 2013), whereas disrupting the quality of cutaneous information from the foot can result to poorer upright stance (Fiolkowski et al., 2002; Voudouris et al., 2013). Once confronted with dynamic visual environments, such as with visual motion, the standing sensorimotor system

upweights visual processes (Jeka et al., 2000). However, when the visual input requires a rapid postural response, integration of visual, vestibular, and somatosensory signals is necessary to form a motor plan and elicit a suitable response. In this case, the upweighting of somatosensory afferents may be important, through which one can obtain a better estimate of the current body configuration and plan the appropriate response. In line with this idea, somatosensory processing is modulated around gait initiation, reflected in the facilitation of somatosensory evoked potentials (Mouchnino et al., 2015).

In this study, we examined sensory and motor adjustments during upright stance. Participants were standing and immersed inside a virtual room, facing a wall that would sometimes be moved towards them. We introduced predictable or unpredictable visual perturbations and measured the effects on postural control and tactile sensitivity. We expected reduced sway in anticipation to the predictable perturbation (Eikema et al., 2013), and distinct body reactions after the perturbation. We also hypothesized modulation of tactile signals from the participants' leg (Morita et al., 1998). Specifically, we expected tactile suppression when coping with perturbations compared to standing quietly, and stronger suppression before the predictable than the unpredictable perturbation (Voudouris et al., 2019). Lastly, we hypothesized a temporal modulation of tactile suppression: If suppression reflects an interplay between feedback and feedforward signals, suppression should be weaker at moments when sensory guidance of the movement is deemed more important (Voudouris & Fiehler, 2021).

Methods

Experiment 1

Participants and apparatus

We recruited 20 participants (24.4 ± 4.8 years old; range: 19-39, 11 ♀ 9 ♂) for a one-session virtual reality experiment. One additional participant was recruited but did not finish data collection due to circulatory problems. Participants were free from any known neurological or musculoskeletal issues at the moment of the experiment and had normal or corrected-to-normal vision. Upon their arrival, participants signed an informed consent approved by the local ethics committee of the Justus Liebig University Giessen in accordance with the "World Medical Association Declaration of Helsinki" (2013, except for §35, pre-registration). At the end of the experiment, participants received for their efforts either 8€/hour or course credits.

A custom-made vibrotactile stimulation device (Engineer Acoustics Inc., Florida, US), which will be referred to as a "tactor", was attached to the *musculus gastrocnemius lateralis* of the participant's right calf. This tactor was fixed at 3 cm medial of 2/3 of an imaginary line connecting the heel with the *caput fibulae.* Thus, the tactile device was fixed on the muscle belly. Care was taken that loose wires or clothing could not be mistaken as vibrations and that they would not hinder the performance of the task. Participants stood barefoot or with their socks on having their feet closed together on a force plate (AMTI, Massachusetts, US) that sampled the center of pressure (COP) with 300 Hz. They also wore a head-mounted display (HTC Vive Pro Eye, Taiwan) that presented a virtual environment and sampled positional data at a rate of 90 Hz. Participants were then immersed in a 3 x 3 x 6 m (width, height, depth) room with black and white striped side walls and a grey front wall. At 1.85 m above the floor, a circular fixation point with a 60 cm radius was presented (Figure 1). The virtual environment was a custom-made Unity version 2021.3.4f1 (Unity Technologies, San Francisco, US) build.

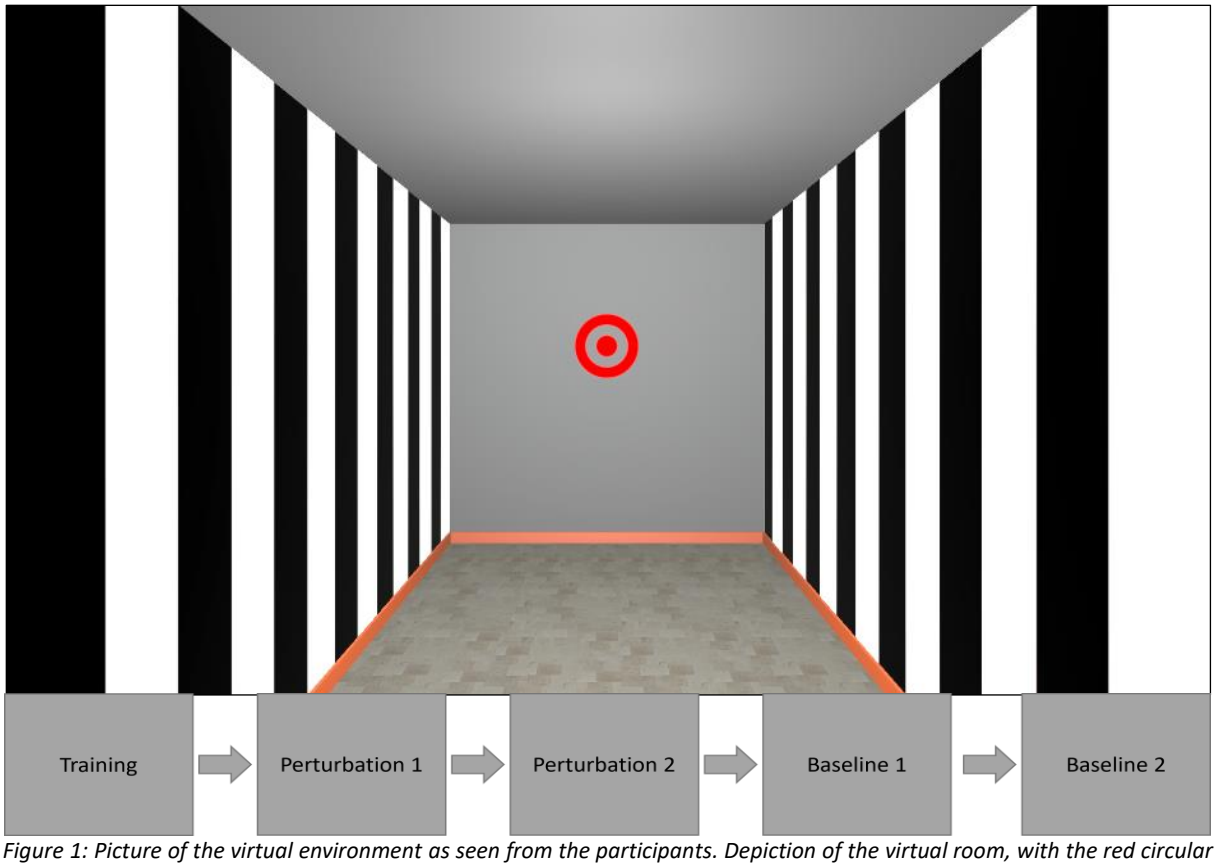

Figure 1: Picture of the virtual environment as seen from the participants. Depiction of the virtual room, with the red circular fixation point appearing at the front wall. The lower panel shows the block order.

Participants stood upright on the force plate with their arms relaxed at their side, and were asked to fixate the fixation point at all times. In most of the trials, a visual perturbation was induced by having the front wall move toward the participant. At different time points within each trial, a brief vibrotactile stimulus was presented on the leg, and participants had to verbally report whether they detected this stimulus or not. This procedure is commonly used to probe tactile suppression (Colino & Binsted, 2016; Voudouris & Fiehler, 2021), and the perception of this probing stimulus is used as a proxy to quantify the relative contribution of predictive and feedback signals (Voudouris et al., 2019; Fuehrer et al., 2022).

Procedure

The experiment consisted of five separate blocks of trials, with each trial lasting 7 s. The first block was always a set of training trials. Here, a countdown (3, 2, 1) appeared above the fixation point on the front wall, with each digit being presented for 0.75 s. At the end of this countdown, a visual perturbation occurred, which consisted of the complete room moving in such a way that the front wall approached the participant with a velocity of 3 m/s for 5 m. After each trial, the room instantly recovered back to its original configuration. After this training block, two perturbation conditions were presented in a random order across participants. In each of these two blocks, the room could be

perturbed in a temporally predictable or unpredictable way. In the predictable condition, trials started with a fixed delay of 0.75 s, followed by a 2.25 s period of countdown, and the visual perturbation occured immediately after that countdown. In other words, the perturbation occured 3 s after the onset of the trial, identically to the perturbation in the training block. In the unpredictable condition, a trial would start without a countdown, and the perturbation would occur within a random moment between 2.25 and 3 s from the beginning of the trial. The absence of the countdown and the 0.75 s random delay increased the uncertainty about the exact moment of the perturbation. These resulted in a difference in the predictability of perturbation onset between these two conditions, while also allowing us to capture the time window during which the countdown appeared (so people could anticipate) in both perturbation conditions. Upon completion of these two perturbation conditions, two blocks followed where we assessed baseline sensory and motor performance: one block with and another block without a visual countdown, but importantly both blocks without any visual perturbation. In other words, these two baseline conditions were identical to the two perturbation conditions but now the virtual room never moved. The order of the two baseline conditions was identical to the order of the perturbation conditions, and this order was randomized across participants. Participants were explicitly informed prior to the onset of each block about the conditions that they would be exposed to.

To probe tactile sensitivity, we delivered a brief (50 ms, 250 Hz) vibrotactile stimulus of varying intensities at the participants' right calf muscle at various moments during each trial, and participants had to report whether they felt a vibration or not. This procedure is used as a proxy to assess tactile sensitivity and how this is affected by a various factors (e.g., Buckingham et al., 2010; Colino & Binsted, 2016; Voudouris & Fiehler, 2021). In the two perturbation conditions, the probing tactile stimulus was delivered at a random moment during one of three possible intervals relative to perturbation onset: two at the pre-perturbation period ("early": -2.25 to -1.50 s, and "late": -1.50 to -0.75 s) and one at the post-perturbation period ("after": 0.00 to 0.75 s; Figure 2). We presented 30 trials at each of these three intervals for a total of 90 trials per perturbation block. The order of the stimulation interval was randomized within each block. In each of the training and two baseline conditions there was a single time interval during which the tactile probe could be presented. For the training and predictable baseline condition it was between 0.75 – 3.75 s, whereas for the unpredictable baseline condition, this was between 0 – 3.75 s, always relative to the onset of the trial.

The intensity of vibration in each trial was determined using a QUEST algorithm (Psychtoolbox Version 3.0.18). As a Bayesian approach, the QUEST algorithm uses prior knowledge to estimate the parameters of a psychometric function (Watson & Pelli, 1983). We assumed a Weibull function with β=3.5 also known as Weibull-slope. The prior mean and standard deviation for the training block were estimated from a pilot study where participants just stood with their feet closed (N=16, exposed to 50

stimuli of varying intensities, presented at the right calf muscle). We used the mean of the estimated probability density function as probe intensity for the next trial. For all the other conditions we used the estimated threshold of the training block as prior mean.

In each trial, participants were instructed to verbally report whether or not they felt a vibration. They were instructed to immediately respond once they felt a vibration to avoid memory effects, but they were also explicitly asked to respond after the trial ended if no answer was meanwhile given. These verbal responses were then registered by the experimenter via button presses to a computer, which induced a small delay (0.5 – 1 s) between trials. To prevent fatigue, participants could have a break after every trial on request. Breaks of ~1 minute were enforced every 30 trials and longer breaks of ~5 minutes were introduced after 90 trials. During these longer breaks, participants were required to sit and were allowed to remove the headset. This resulted in a duration of around 20 minutes for each perturbation block, with a total experimental time of 90 minutes. Trial control, data acquisition, and data analysis were handled by custom-made Matlab R2021a software (The Mathworks, Massachusetts, US).

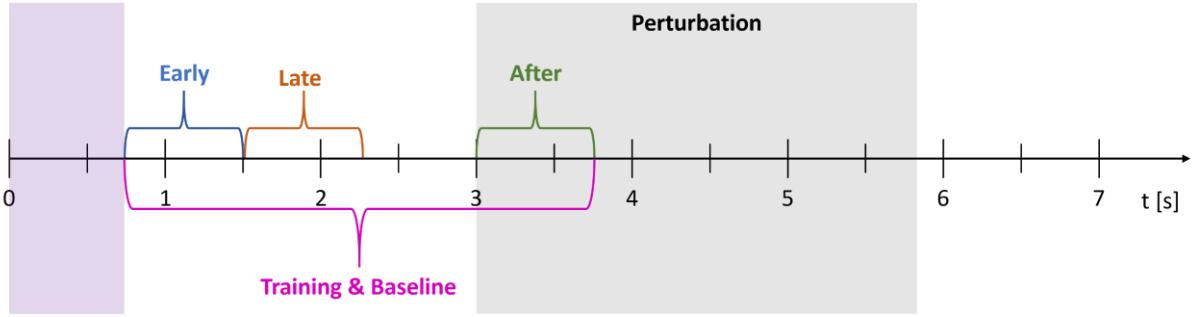

Figure 2: Schematic timeline of a single trial of the perturbation condition. The timeline goes from 0 to 7 seconds. The probe tactile stimulus in the two perturbation blocks could be presented at one of three possible intervals: "early" (blue), "late" (brown), and "after" (green), whereas in the baseline and training conditions it could be presented at any moment during a single interval (purple). The onset of the perturbation is depicted here at the 3rd second of the trial, but this could vary in the condition with the unpredictable perturbation.

Data analysis

The COP and headset kinematics were analyzed only in the anterior-posterior (negative to positive values, respectively) direction as the visual perturbation happened in this direction. In a first step, we excluded trials with gaps exceeding 100 ms (1.2%). Afterwards we normalized every sample of each trial to the average position of the first 0.5 s of that trial, which we consider as a period of quiet stance, because there was nothing happening to the room. The resulting normalized data was corrected for outliers by replacing values with a displacement larger than 15 cm with the median of this trial's timecourse, and then smoothed utilizing a symmetric moving average with a window size of 100 ms.

Anticipatory kinematic adjustments were quantified as the maximum absolute COP and head amplitude during the last 2.25 s prior to perturbation onset. To quantify reactive kinematic behavior

we first determined the maximum positive (posterior) COP and head displacement during the first 3.5 s following the onset of the perturbation. This corresponds to about 2 times the perturbation duration. Determining the maximum COP and head position values was important because any reaction to the perturbation would result in the body leaning backward and thus to a positive COP and head position value. We then quantified reactive kinematic adjustments of the COP and head as the difference between their maximum value and their respective minimum that occurred between the perturbation onset and that maximum (see Figure 3). Both of the previous measures were normalized with respect to the values calculated from their respective baseline periods (quiet stance), to account for individual differences in standing. Thus, values greater than zero indicate larger displacements during the perturbation blocks relative to the respective baseline.

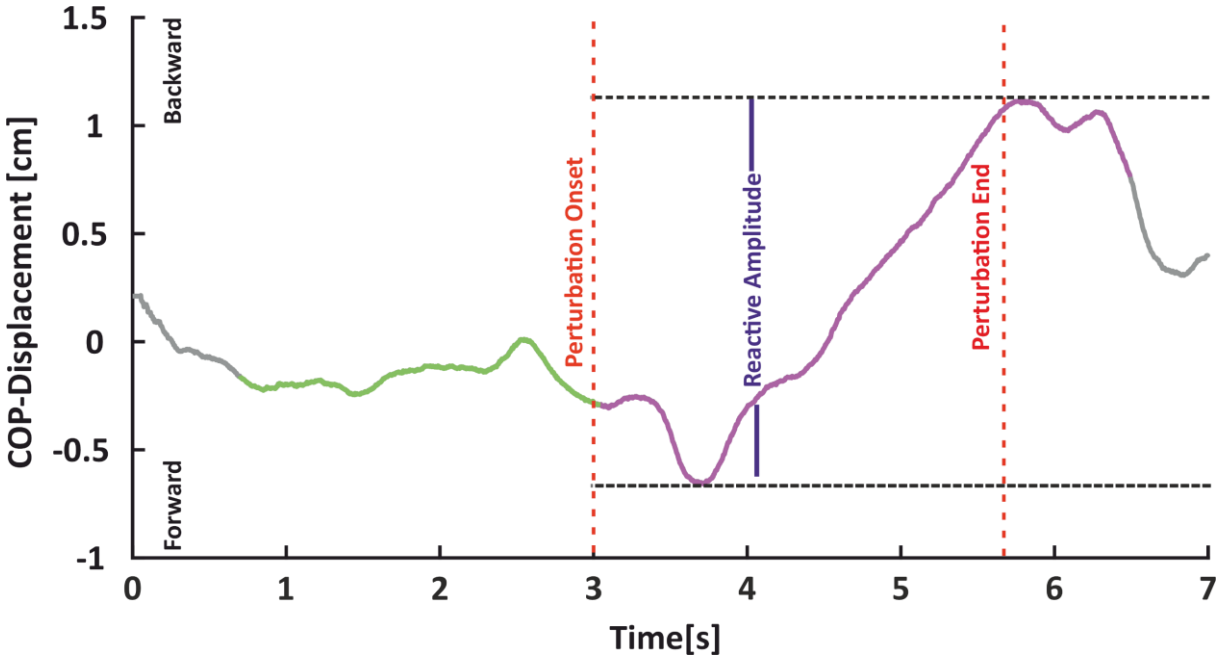

Figure 3: Temporal profile of the CoP time course in the antero-posterior direction of a predictable trial. The time window of perturbation (red dashed lines), the anticipatory period (green path), the reactive period (purple path), and the reactive amplitude (blue solid line) are depicted.

We determined tactile detection thresholds for each condition and participant. For this, we first screened the responses given by the partcipants for validity. We then determined the point of convergence as the first trial after which the probe stimulus intensity recommended by the QUEST did no longer change value. We expected some fluctuation in the responses after the point of convergence due to natural randomness in the responses. For this reason, we considered detection thresholds as invalid if more than 99% of the trials after the point of convergence had the same response. These thresholds (4.2%) were excluded from further analysis. To quantify tactile modulation while also accounting for individual differences in tactile sensitivity, we subtracted each participant's baseline

detection threshold from their threshold obtained at each time interval of the respective perturbation block (Δthreshold), a procedure in line with previous work (Fuehrer et al., 2022).

Statistical analysis

We first examined whether anticipatory behaviour was evident prior to perturbation compared to baseline by testing if the maximum discplacement in head and COP kinematics deviated from the respective values during quiet stance. Because we subtracted the maximum displacement in baseline from the respective value in the perturbation blocks, we quantified possible effects by using two-sided one-sample t-tests against zero. Similarly, we tested whether the reactive component in each perturbation condition deviated from zero. Our main interest was whether tactile perception would be tuned to the predictability of the perturbation and the probing moment. To investigate possible effects of predictable and unpredictable perturbations on tactile processing, we submitted the obtained Δthreshold values to six separate two-sided one-sample t-tests against zero (i.e. baseline). To test for possible effects of the type of perturbation (predictable, unpredictable) as well as of the time interval of the tactile probing ("early", "late", "after") on tactile processing, we used a 2x3 repeated measure ANOVA. Significant main effects were explored with post-hoc t-tests, corrected for multiple comparisons wherever necessary using the Holm procedure. All t-values are reported as absolute values. The type one error threshold was set to 0.05 and effect sizes are reported as η^2 following the calculations and recommendations from Correll et al. (2020). Statistical analyses were conducted in JASP version 0.17.1 (University of Amsterdam, Netherlands).

Experiment 2

In Experiment 1 we examine the temporal modulation of tactile processing when coping with predictable and unpredictable visual perturbations of upright stance. To this end, we compare tactile perception when standing and being confronted with a perturbation to when standing without having to cope with any perturbation. However, standing itself may already influence tactile processing on the leg. To account for this possibility, we conducted Experiment 2, wherein we test the influence of quiet stance on tactile detection thresholds.

Participants and experimental design

We recruited 10 new participants (25.3 ± 4.0 years old; range: 21-32; 9 ♀ 1 ♂) for a one-session experiment, while two additional participants did not finish data collection due to circulatory problems or incompliance with task instructions. The procedure was almost identical to Experiment 1, but now

participants performed six blocks of trials: a training block, two perturbation blocks, two standing baselines, and after these, an additional sitting baseline. During this sitting baseline, participants wore the head mounted display and sat relaxed on a chair with their knees flexed at ~90 deg and both feet touching the floor. In this sitting baseline, participants performed 30 trials that were constructed identically as in the other two standing baseline blocks. In all six blocks of Experiment 2, participants saw exactly the same room as in Experiment 1. The experimental procedure and analyses were identical to those reported for Experiment 1, except for the details mentioned below.

Data and statistical analysis

As we were interested in the modulation of tactile processing by standing, we focused our analysis on tactile detection thresholds. In contrast to Experiment 1, detection thresholds that were obtained during the two perturbation blocks were now normalized with respect to the new sitting baseline, resulting again in six Δthreshold values per participant. The screening of detection thresholds for validity resulted in excluding 1.7% of them. Furthermore, and since we did not observe any differences in the two standing baselines in Experiment 1 (t_{19} = 0.621, p = 0.542, η^2 = 0.005) or Experiment 2 (t_9 = 0.263, p = 0.798, η^2 = 0.002), we now averaged across the two (predictable and unpredictable) standing baselines thresholds for each participant.

A two-sided paired t-test was performed to test for differences between the standing and the sitting baselines. To examine whether tactile signals are suppressed during the perturbation blocks relative to the sitting baseline, we constrasted the Δthreshold values against zero (i.e. baseline) with six separate one-sided one-sample t-tests. All t-values are reported as absolute values. Additionally, we submitted the Δthreshold values to a 2x3 repeated measure ANOVA to investigate for main effects of predictability of perturbation (predictable, unpredictable) and time of probing (“early”, “late”, “after”) on tactile modulation.

Results

Experiment 1

Kinematics

Anticipatory postural control was generally evident prior to the predictable perturbation compared to the respective baseline. Specifically, the COP maximal displacement was smaller than that during the respective baseline (t_{19} = 2.184, p = 0.042, η^2 = 0.056; Figure 4A), in line with our hypothesis based on previous work (Eikema et al., 2013). The head maximal displacement was also smaller before the predictable perturbation compared to that during the respective baseline (t_{19} = 2.738, p = 0.013, η^2 = 0.086; *Figure* 4B). Meanwhile, there was no evidence of anticipatory behavior prior to the unpredictable perturbation, as reflected both in the COP and the head maximal displacements (t_{19} <= 0.264, p >= 0.455, η^2 <= 0.007). These findings confirm that participants considered the underlying dynamics of the perturbations and tuned their posture predictively whenever possible.

Unsurprisingly we found higher sway amplitudes in the reactive compared to the baseline period in the unpredictable condition, as reflected in the COP (t_{19} = 4.489, p < 0.001, η^2 = 0.201) and the head kinematics (t_{19} = 3.950, p < 0.001, η^2 = 0.163). Likewise, sway amplitudes were larger in the reactive than baseline period of the predictable condition, evident mainly in the COP (t_{19} = 2.286, p = 0.034, η^2 = 0.061) while the head kinematics were more variable (t_{19} = 1.756, p = 0.095, η^2 = 0.037). These results indicate a compensation of the visual perturbation.

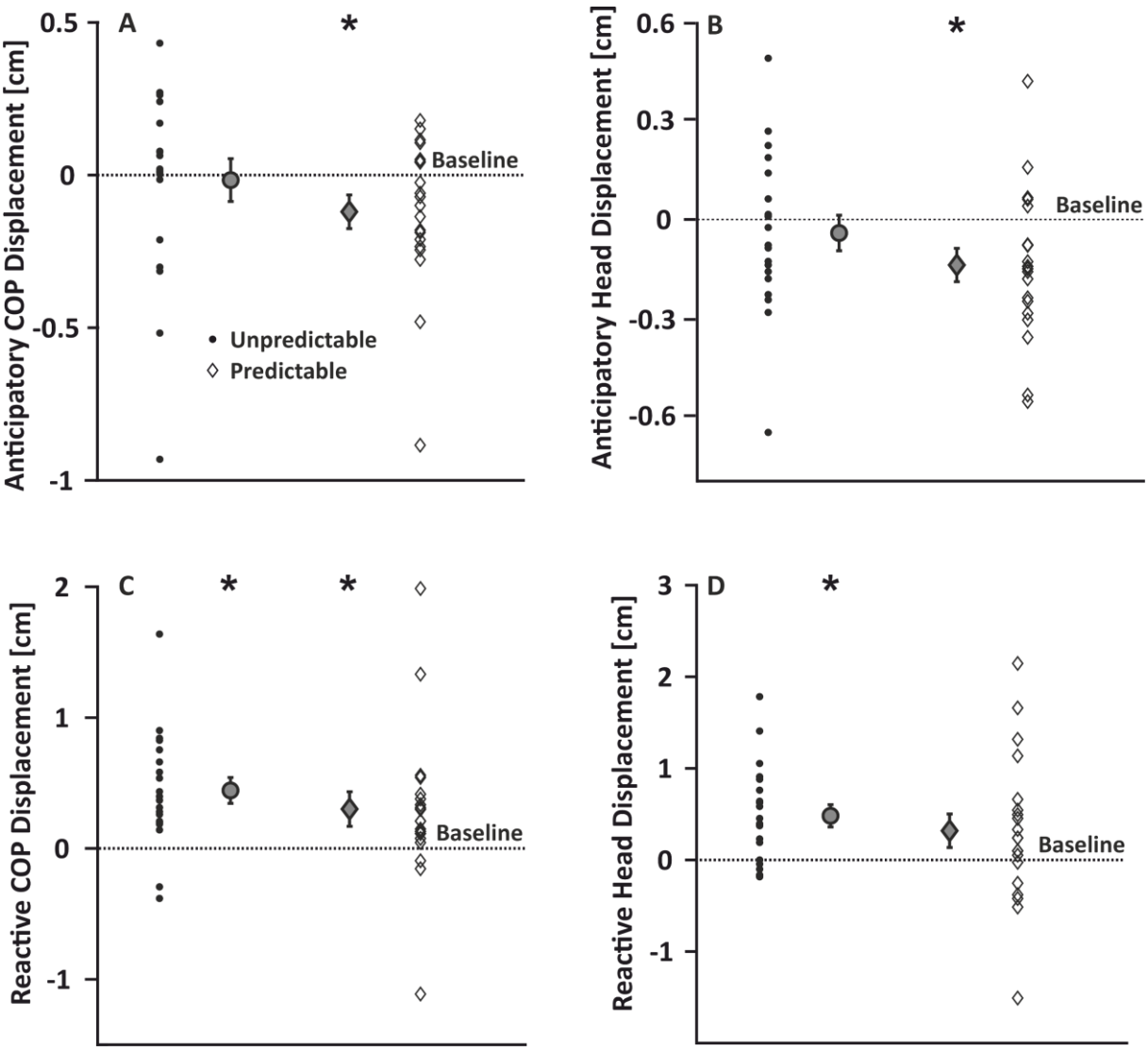

*Figure 4: Kinematic results for the anticipation and reaction period. Panels A and B show anticipatory COP and head kinematic behavior, respectively. Panels C and D show reactive COP and head kinematic behavior, respectively. All four panels show single-subject data for the predictable (diamonds) and the unpredictable (circles) conditions, as well as their corresponding means and standard errors. Dashed lines represent the baseline value and * indicates $p < 0.05$.*

Tactile processing

Figure 5 shows the distribution of the number trials required for the QUEST algorithm to converge, for all 262 valid detection thresholds. With a minimum of 2, a maximum of 18, and on average of 8.3 ± 2.3 trials needed the 30 trials that we presented in each condition were enough to obtain a detection threshold.

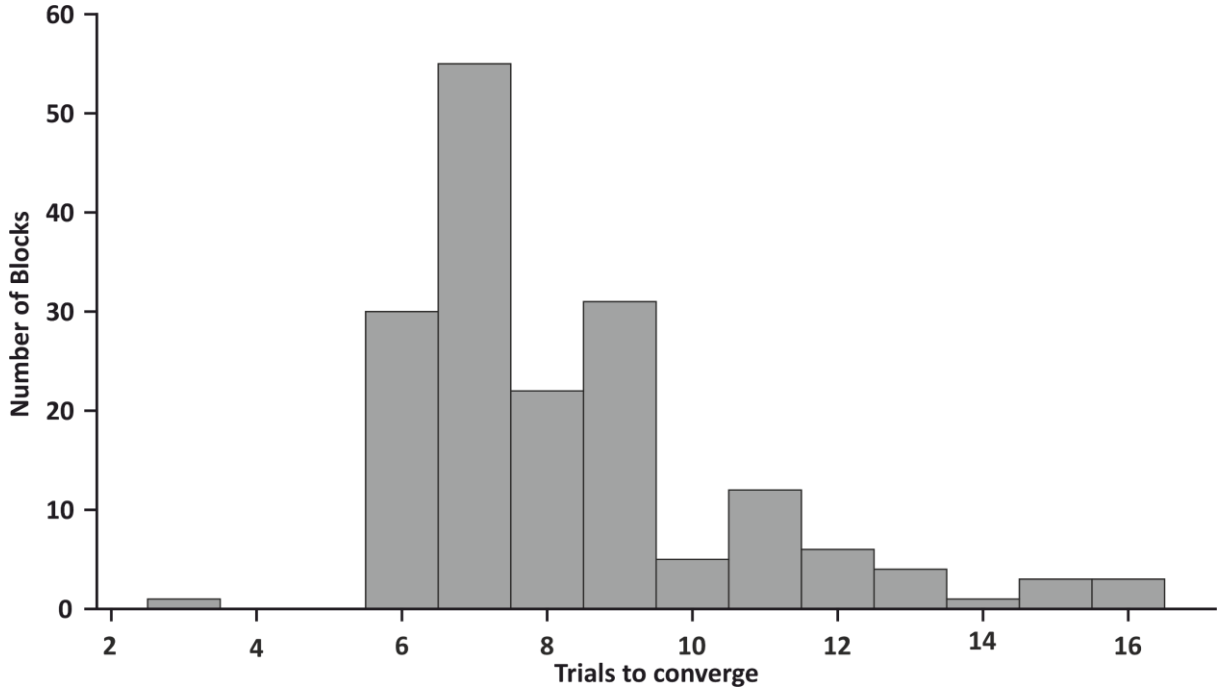

Figure 5: Histogram of the required number of trials to convergence of all valid detection thresholds. The histogram shows cumulative how many trials it took to estimate the 262 detection thresholds obtained in all conditions of the experiment.

Although some detection thresholds during the perturbation blocks appear to be different from the respective baseline, none of the detection thresholds was systematically affected (all t <= 1.933, all p >= 0.069, η^2 <= 0.047). This is at odds with previous findings that show tactile modulation during arbitrary (Voss et al., 2008) and goal-directed movements (Buckingham et al., 2010), and even around the initiation of gait (Mouchnino et al., 2015).

There was no effect of predictability on the Δthreshold values ($F_{1,14}$ = 0.036, p = 0.556, η^2 = 0.012; Figure 6), but there was a main effect of time ($F_{2,28}$ = 4.364, p = 0.022 η^2 = 0.054). Post hoc t-tests revealed significantly higher detection thresholds in the "early" compared to the "after" interval (t_{18} = 2.942, p = 0.019, η^2 = 0.064), but similar thresholds between the "late" and "after" (t_{18} = 1.699, p = 0.201, η^2 = 0.022) and between the "early" and "late" intervals (t_{18} = 1.243, p = 0.224, η^2 = 0.012). This indicates that tactile sensitivity improved at the period after the onset of the visual perturbation, at least relative to the "early" pre-perturbation period. There was no interaction between predictability and time ($F_{2,28}$ = 0.190, p = 0.828, η^2 = 0.004).

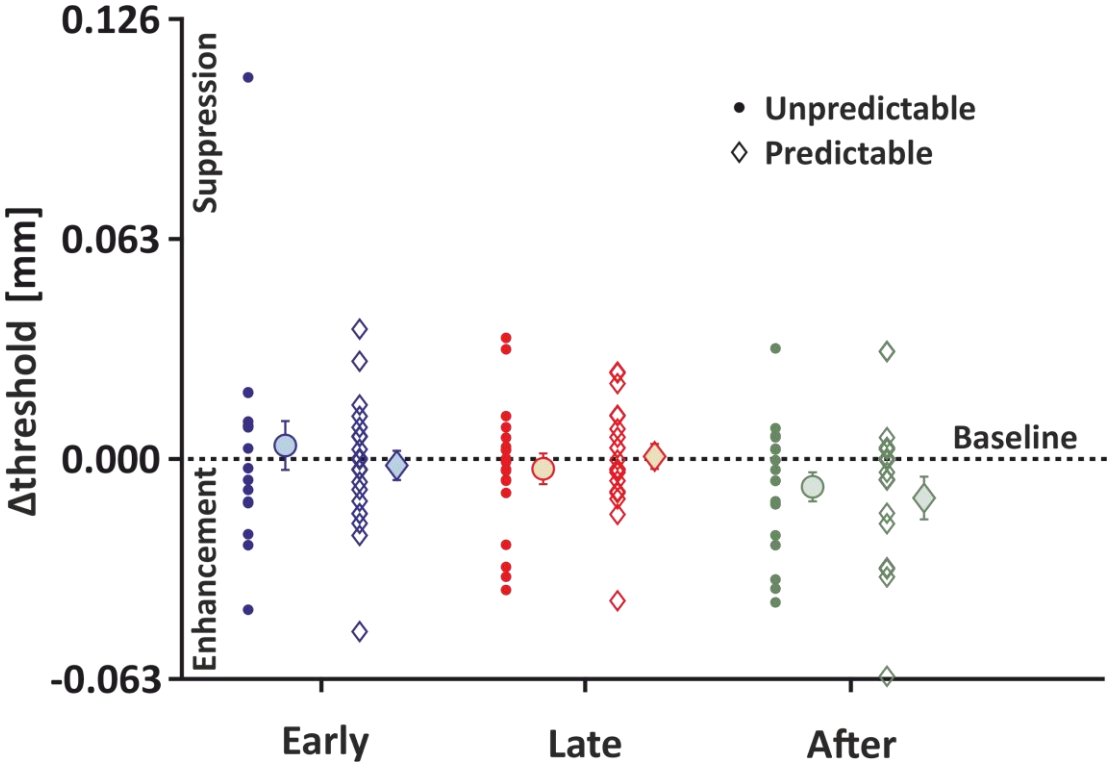

Figure 6: Normalized detection thresholds during the perturbation blocks (Δthreshold). Comparison of normalized detection thresholds for the three time intervals of the unpredictable (circles) and predictable (diamonds) conditions. Single subject data relative to their respective standing baseline as well error bars with the means and standard errors are depicted.

Experiment 2

We conducted experiment 2 to test if standing is already causing tactile suppression and therefore marginalizing any possible additional effects on suppression that arise around the visual perturbation. To this end, we first contrasted tactile perception during quiet stance against sitting. Tactile suppression was evident during standing than sitting (t_9 = 2.285, p = .048, η^2 = .115; Figure 7). Additionally, tactile signals were suppressed relative to sitting at all three time intervals of each predictability condition (all t >= 2.213, all p <= .027, all η^2 >= .109). These show clear tactile suppression during quiet stance and around the visual perturbations compared to sitting.

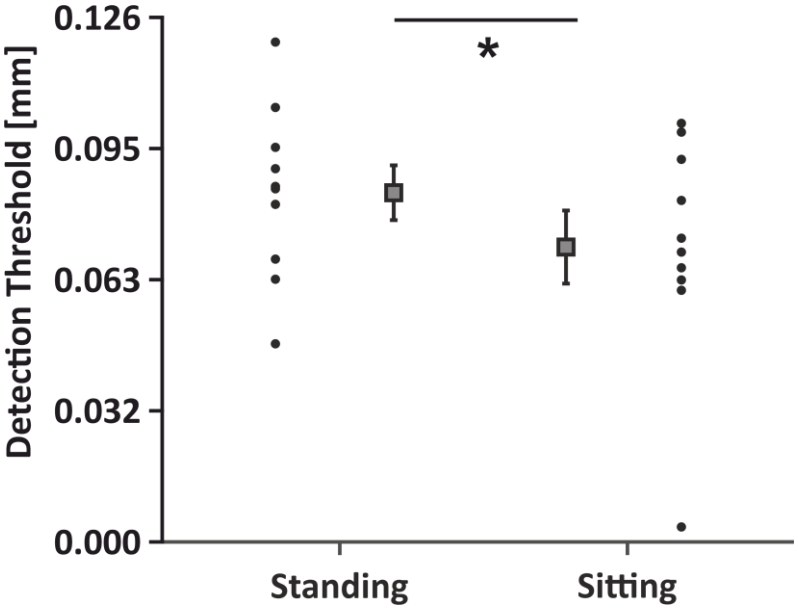

*Figure 7: Comparison of raw detection thresholds between standing and sitting. This graph shows the detection thresholds for standing (left) and sitting (right). Single subject data is depicted with dots, whereas averages and standard errors are shown with squares and the respective error bars. * indicates p < 0.05.*

As in Experiment 1, the 2x3 ANOVA revealed a main effect of time ($F_{2,16}$ = 8.638, p = 0.003, η^2 = 0.121; Figure 8), showing that suppression was dynamically modulated throughout the trial. Suppression was higher in the "early" ($t_8 = 4.109$, $p = 0.002$, $\eta^2 = 0.084$) and "late" ($t_8 = 2.595$, $p = 0.039$, $\eta^2 = 0.035$) periods compared to that after the perturbation, but was similar between the "early" and the "late" periods ($t_8 = 1.514$, $p = 0.149$, $\eta^2 = 0.012$). These are in line with the findings of Experiment 1, and suggest an improvement in tactile feedback processing at moments when sensory guidance of postural reactions gain importance. There was no main effect of predictability ($F_{1,8}$ = 0.502, p = 0.499, η^2 = 0.029), nor an interaction ($F_{2,16}$ = 1.541, p = 0.244, η^2 = 0.045).

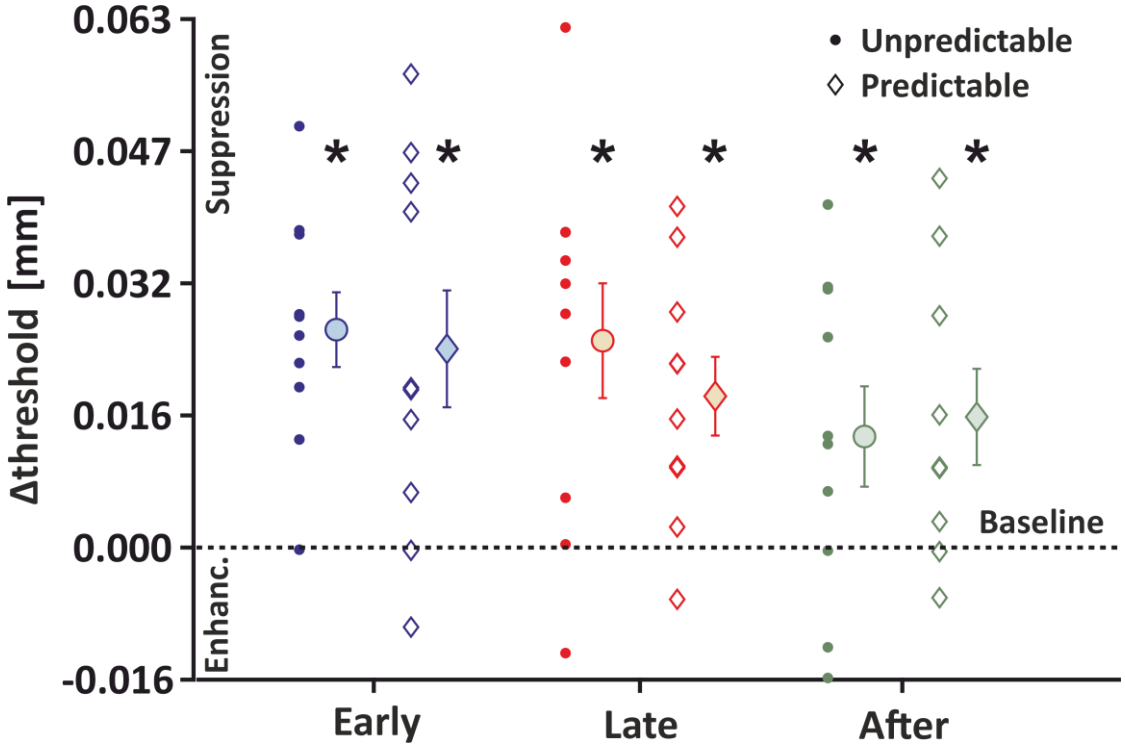

*Figure 8: Temporal modulation of normalized detection thresholds to the sitting baseline (Δthreshold). Comparison of normalized detection thresholds for the three time intervals of the unpredictable (circles) and predictable (diamonds) conditions. Single subject data relative to their respective standing baseline as well as error bars with the means and standard errors are depicted. * indicates $p < 0.05$ from the sitting baseline.*

Discussion

We examined postural control and tactile modulation during complex whole-body movements in dynamic environments. Therefore, we used a virtual adaption of the classical moving room paradigm that allows for cost-efficient studies in naturalistic environments. This enabled us to manipulate the predictability of the environment and examine the temporal modulation of postural and sensory responses to new visual information. Specificially, we introduced visual perturbations those timing was either predictable or unpredictable. As expected (Eikema et al., 2013), when perturbations were predictable, participants predictively tune their posture by stiffening up their body, reflected in reduced displacement of the COP and the head movement. We also confirmed that participants react to new visual information by compensatory COP and head adjustments that arise after the perturbation, and independently of its predictability. This effect was mainly evident in the COP modulation and not in the head kinematics suggesting that the motor system prioritizes the stabilization of the head over that of the trunk (Berthoz & Pozzo, 1994).

Second, we examined the influence of the temporal dynamics and the predictability of the visual perturbationson tactile sensitivity. Although we did not observe any effects of the predictability of perturbation, tactile sensitivity was temporally tuned throughout the trial showing enhanced sensitivity after the onset of the perturbation. This is in line with previous findings that found improved tactile processing at moments when the sensory control of movement gains importance (Mouchnino et al., 2015; Voudouris & Fiehler, 2021). We here expand these findings by demonstrating temporal tuning of tactile signals from the standing leg, in two independent samples, which suggests a reliable effect. Tactile processing from the standing limb was improved after the onset of the visual perturbation, independently of whether this perturbation was predictable or not. This indicates an upweighting ofsomatosensory processing from the standing limb, reflected in the perception of the probe tactile stimulus, just before a body movement is initiated to counteract the visual perturbation. The temporal modulation of tactile processing when standing is in line with previous findings showing temporal tuning of tactile processing during goal-directed hand movements (Colino & Binsted, 2016; Voudouris & Fiehler, 2021). The improved tactile sensitivity shortly before the initation of the reactive body movement extends previous work by showing facilitation of cutaneous information from the standing leg shortly before a step is initiated (Mouchnino et al., 2015). We suggest that the mechanism underlying this temporal modulation is similar to those proposed in the afore-mentioned studies, and that it reflects the interplay between sensorimotor predictions and somatosensory feedback.

We also hypothesized a modulation of tactile perception based on the predictability of the perturbation. A recent study demonstrated weaker suppression when grasping static objects of unpredictable than predictable dynamics (Voudouris et al., 2019). Such result indicates partial recovery of tactile feedback when somatosensory information from the moving hand is important to work out

the object's properties. That we do not find any effect between predictable and unpredictable conditions might be explained by various possibilities. First, exposure to the dynamics of the visual perturbations might have been too short to influence tactile perception, even though it influenced associated motor behavior, which is in line with recent finding in grasping (Beyvers et al., 2023). Second, the uncertainty about the onset of the unpredictable perturbation might be not large enough to reduce tactile suppression. Third, task demands might have been very high in both conditions leading to a ceiling effect of tactile modulation (Klever et al., 2019).

Interestringly, in Experiment 1, tactile perception was not different between perturbation and quiet stance trials. This is at odds with our expectation that tactile signals would be influenced when being confronted with perturbations. A possible reason for this may be that quietly standing upright already leads to suppression of tactile signals from the standing leg. Indeed, when compared to a sitting baseline in Experiment 2, tactile perception during standing was systematically suppressed. This tactile suppression during quiet stance may stem either from backward masking caused by the activation of the lower-leg muscles, or from predictive processes associated with the control of upright stance, or from a combination of the two. Indeed, standing itself is accompanied by a constant sinusoidal movement (Winter, 1995) and subsequent postural adjustments (Warnica et al., 2014), and when the base of support is reduced, like in our experiments, then muscular activity of the lower leg muscles increases (Amiridis et al., 2003). Such increase in peripheral activity may mask the probing tactile stimuli that we presented (Williams & Chapman, 2002; Chapman & Beauchamp, 2006). However, so far there is no clear evidence that increases in the muscular activity can modulate tactile suppression (Broda et al., 2020). Thus, the suppression of tactile signals from the leg when standing likely reflects a process associated with efferent motor commands for the continuous control of posture.

We demonstrate tactile suppression during standing relative to the sitting baseline. This sitting baseline block occurred always at the end of the experimental procedure. One possibility, therefore, might be that the reported tactile suppression is a byproduct of improved tactile detection perception at the later blocks due to practice. This could lead to lower detection thresholds toward the end of the experiment compared to the preceding standing tasks, and so the suppression might be unrelated to feedback or feedforward processes. However, we think this is unlikely to happen for two reasons. First, the standing baseline tasks in Experiment 1 did not yield lower detection thresholds than the earlier-presented perturbation tasks. Thus, the lower detection thresholds during sitting in Experiment 2 are unlikely to arise simply because of a longer exposure to the tactile task. Second, tactile detection thresholds, at least on the hand, are similar between sessions separated by 30 min (Voudouris & Fiehler, 2022). All in all, the reported effects are unlikely to be caused by a possible improvement in the performance of the tactile task over the course of the experiment.

Our results expand previous work on tactile suppression by demonstrating hampered tactile processing during more complex, whole-body movements in dynamic environments, as well as a temporal modulation of this suppression when coping with visual perturbations. These results provide further evidence for the idea that tactile suppression stems from an interplay in the weighting of predictive and feedback signals for the task, with improved tactile processing on a moving body part when somatosensory feedback signals from that part gain relevance for the sensory guidance of the movement.

Data availability

Behavioral and psychophysical data are publicly available after acceptance at https://osf.io/jdzwa/.

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Disclosures

None of the authors has conflicting interests.

Author contributions

Conceived and designed research: F.D.W., K.F., D.V.

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Interpreted results of experiments: F.D.W., K.F., D.V.

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